



Silicon content is a plant functional trait: implications in a changing world[☆]

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ABSTRACT

Plant silicon (Si) content is a trait that has gained increasing attention in recent years, and is now often suggested to be a plant functional trait. This paper reviews the evidence that supports the inclusion of plant Si content within the plant functional traits framework. Plant Si contents can vary greatly among plant taxa and environments, reflecting multiplicity of roles and functions in plant biology. Plant Si uptake and accumulation also affects plant community and ecosystem properties, and thus ecological functioning and response to environmental change. Further investment in studying plant Si content as a plant functional trait and its roles in ecological processes will improve our ability to predict and mitigate the consequences of climate change.

1. Introduction

Plant functional traits are traits that indirectly influence the fitness of an individual via their effects on its growth, reproduction and survival (Garnier et al., 2016), whose values vary in response to environmental conditions and affect ecosystem functioning (Funk et al., 2017; Garnier et al., 2016), and are often taken as any morphological, physiological or phenological feature, measurable for individual plants, at the cell to the whole-plant level (Perez-Harguindeguy et al., 2013). Thus, plant functional traits are pivotal in linking environmental changes with plant community and ecosystem properties, functioning and responses (Diaz et al., 2004; Funk et al., 2017; Garnier et al., 2016; Violle et al., 2014). Therefore, the study of plant functional traits can enable us to quantitatively describe how environmental variables affect plant trait values and how plant trait values affect ecosystem functioning (Garnier et al., 2016). Consequently, such analyses can provide parameters required to directly model and predict – and hopefully mitigate – the effects of environmental change on ecosystem functioning (Fig. 1). This is a major objective in these times of climate change.

Studies of plant functional traits so far have focused almost entirely on morphological, physiological and phenological traits, or on the contents of essential macronutrients such as nitrogen and phosphorus (e.g., lists in Garnier et al., 2016; Perez-Harguindeguy et al., 2013). Nevertheless, many plants also contain appreciable amounts of non-essential but beneficial nutrients that are known to affect plant fitness and environment, and whose contents within the individual plant are driven by (i.e., respond to) the environment. These traits have been

mostly ignored in plant functional traits literature. For example, many plant taxa are known to accumulate silicon (Si) in their tissues, often as various amorphous phases including silicon double layers (e.g., Schaller et al., 2013) and microscopic bodies of Opal-A ($\text{Si}(\text{OH})_2 \cdot n\text{H}_2\text{O}$) called phytoliths (e.g., Hodson et al., 2005). Here, I review the evidence that plant Si content is a plant trait whose multiple functions in plant response to environmental factors, effects on plant performance, and effects on plant communities and ecosystems has gained increasing appreciation in recent years. The accumulation of such evidence suggests that plant Si content is a plant functional trait that can contribute to models of environmental change effects on ecosystem functioning and potentially to improve their predictive power. Although this idea has been expressed both implicitly and explicitly by some (Cooke and Leishman, 2011a; Cooke et al., 2016; Katz, 2014, 2015; Schoelynck and Struyf, 2016; Schoelynck et al., 2014), elaborate discussions of the potential use of plant Si content as a mediating plant functional trait in predictive models are missing. I wish to set the step stones to these discussions here.

In this short review, I demonstrate the case for Si content as a plant functional trait. I first discuss the variability of Si contents among plants and environments, which demonstrates its correspondence with other plant functional traits and response to the environment. I then discuss plant Si's roles, from individual plants to the entire ecosphere, and how this trait and its functions may have evolved over geologic time. Finally, I discuss major knowledge gaps that, if filled, will improve understanding, monitoring, predicting and mitigating climate change effects on plant communities and ecosystems.

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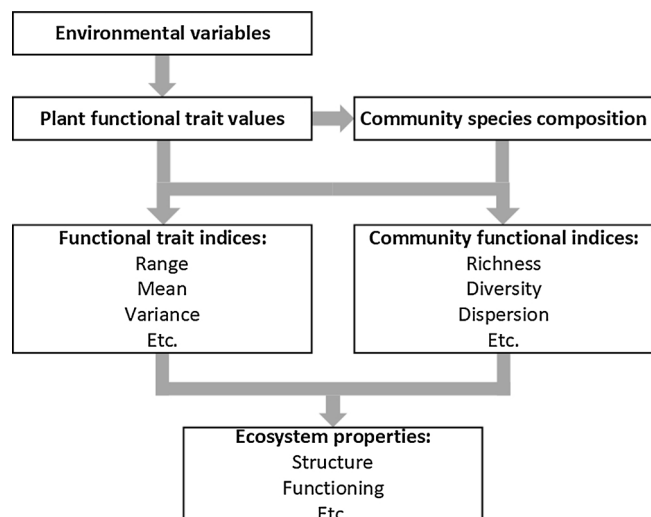


Fig. 1. A simplified model of the plant functional diversity approach. Environmental variables (and especially abiotic ones) act as filters on plant functional trait values. In turn, plant functional trait values drive plant community species composition, together with biotic filters (e.g., competition). Plant community species composition and species functional trait values determine, together, functional trait indices (for each trait) and community functional diversity indices (for trait assemblages). The latter two drive ecosystem properties through the effects of individual species or of species assemblages.

2. Variability of plant Si contents

Although data is still missing for many plant families (Katz, 2015), it is clear now that Si contents vary greatly (to as many as 2–3 orders of magnitude, from nearly 0% to over 10% of plant dry weight) among plant families, orders and phyla (Hodson et al., 2005; Katz, 2015; Trembath-Reichert et al., 2015). Hodson et al. (2005), for example, found that taxonomic order accounts for 67% of interspecific variability in Si contents among seed plants. The sources of this variability remain obscure and somewhat disputed (Katz, 2015; Strömberg et al., 2016). From an evolutionary ecology perspective, one would expect a trait to persist within a clade if it confers some advantage expressed in improved fitness. These implies that taxonomic variability can be explained by ecological roles and functions. However, the roles and functions of plant Si and the variations in their extent among taxa with varying Si contents are not always properly understood (Cooke and Leishman, 2011a; Katz, 2014, 2015; Strömberg et al., 2016).

The variability of plant Si contents is reflected in its trade-offs with other plant components. It has long been known that Si contents are higher in grasses – and more generally in most commelinid monocots – than in non-commelinid monocots and dicots (Hodson et al., 2005; Katz, 2015; Trembath-Reichert et al., 2015). In contrast, calcium oxalate crystals – another inorganic plant component comparable to phytoliths in function – are considerably more abundant in non-commelinid monocots and dicots than in commelinid monocots (Franceschi and Nakata, 2005; Prychid and Rudall, 1999). This contrast suggests a trade-off between plant Si and calcium contents, which appears reasonable since phytoliths and calcium oxalate crystals are thought to play comparable roles in plant structural support and defence against herbivores (see reviews in Cooke and Leishman, 2011a; Franceschi and Nakata, 2005; and further discussion of Si roles in plants below).

No less striking is the evidence for trade-offs between Si and carbon (C)-based plant components. Raven (1983) was among the first to suggest such a trade-off, estimating the metabolic cost of Si-based mechanical support to be 10–20 times less than that of lignin. Thirty years later, a trade-off of Si content with lignin and cellulose contents was found (Klotzbücher et al., 2018; Schoelynck et al., 2010) and

convincingly attributed to plant structural support (Schoelynck et al., 2010). Plant Si content was also found to be negatively correlated with C and phenol contents (Cooke and Leishman, 2012; Frew et al., 2016; Johnson and Hartley, in press; Schaller et al., 2012a, b), with leaf nitrogen and phosphorus content (Song et al., 2014) and thus to affect plant stoichiometry (Schaller et al., 2012a, 2016a; Song et al., 2014). Put together, there is a reasonable case for Si partially substituting C in plant biology (Cooke and Leishman, 2011a). Nevertheless, evidence for Si:C trade-offs are meagre and come from only a few ecosystems but not from regional- or global-scale analyses (Cooke and Leishman, 2011a; Klotzbücher et al., 2018; Schoelynck et al., 2010), and so far lack evidence for clear effects on fitness or explanatory driving mechanisms. Therefore, further evidence is required to validate the partial substitution of C by Si.

Notwithstanding that a plant's Si content is driven by its taxonomy, phylogeny and physiology, the plant's Si content is also driven by its environment. Intraspecific variations in plant Si contents have been studied for many years, mostly in the highly Si-rich grasses. Plant Si content has generally been shown to increase, for example, with transpiration (Euliss et al., 2005; Faisal et al., 2013; Katz et al., in press) and herbivory intensity (Brizuela et al., 1986; Hartley, 2015; Hartley and DeGabriel, 2016; Katz et al., in press; Massey et al., 2008). Plant Si contents responses to water availability are less predictable, and it may be that plant Si content increases towards both extremely arid and rainier conditions (Katz et al., 2013; Quigley and Anderson, 2014).

Apart from the obvious dependence on Si supply, most focus so far has been put on the effects of water availability and herbivory (Katz et al., 2013, 2014, in press). This is a mirror reflection of the extensive studies of plant Si's roles as an adaptation to aridity by reducing water loss, improving water use efficiency and eliciting stomatal responses and antioxidant activity (e.g., Coskun et al., 2016; Gong et al., 2005; Zhu and Gong, 2014) and as an antiherbivory defence due to its low nutritional value and tendency to accumulate as microscopic glass-like silica particles (Correa et al., 2005; Frew et al., 2016, 2017a, 2017b; Hartley and DeGabriel, 2016; Massey and Hartley, 2006, 2009; Massey et al., 2007a; Wiczorek et al., 2015a). Although laboratory experiments tend to demonstrate that plant Si contents are higher at high water availability, extreme drought and strong herbivory pressure, such trends are less frequently found in naturally growing plants (Katz et al., 2013, 2014, in press). Such discrepancies possibly exist because plants that grow in natural ecosystems are exposed to various other confounding variables, including soil silicon and nutrient availability, temperature, transpiration and interactions with other plants, pathogens and animals (in press). They may also stem from interactions among various environmental variables. Moreover, Si may have different roles (e.g., adaptation to aridity, anti-herbivory defence, etc.) in various ecosystems, and to various degrees. This suggests that plant Si content in naturally growing plants may be exposed to natural selection by various agents that do not exist in the laboratory (Garbuzov et al., 2011; Hartley and DeGabriel, 2016; Katz, 2014; Katz et al., 2013, 2014, in press; Quigley and Anderson, 2014; Soininen et al., 2013). Likewise, short-term controlled experiments can seldom account for long-term plant interactions with the environment or for natural selection (Katz et al., 2014; in press; Quigley and Anderson, 2014; Soininen et al., 2013).

Atmospheric CO₂ concentrations may also affect plant Si uptake and accumulation. First and foremost, under higher CO₂ concentrations plants reduce stomatal conductance and hence transpiration as a motive force for Si uptake (Euliss et al., 2005; Faisal et al., 2013). Furthermore, Si:C trade-offs and putative partial substitution of C by Si suggest that at lower CO₂ concentrations plants may invest more in Si-based adaptations, although this has not been demonstrated empirically so far. Evidence for the effect of elevated atmospheric CO₂ concentrations on plant Si contents are inconsistent (Fulweiler et al., 2015; Frew et al., 2017a; Johnson and Hartley, in press; Li et al., 2014), although a negative effect in grasses (Li et al., 2014) may be explained by C

enrichment relieving postulated Si:C trade-off and allowing plants to rely less on Si as a substitute for C.

Different ecosystem types and biomes are often characterised by different plant clades and different strategies (i.e., different trade-offs). With that addition of intraspecific variabilities in plant Si contents along environmental gradients, this suggests that ecosystem types and biomes will differ in plant community Si contents. Carey and Fulweiler (2012), based on Hodson et al. (2005), estimated Si percentages of the total plant biomass for the world's biomes, and found that biomes in which grasses are more abundant tend to be richer in Si (per biomass) and more productive. The mechanisms underlying this pattern are unclear and were not methodically studied so far, but are likely related to the adaptive role of Si in some plant species and Si's high contents in grasses, which are dominant fast-growing species. Nevertheless, at this point in time, the shortage in global-scale empirical field studies of individual plants' and community-level Si contents along large environmental gradients hinders developing global models of how community-level Si contents correspond to environmental variables and how community-level Si contents affect ecosystem functioning (Fig. 1). Once such quantitative knowledge exists, it can be used to parametrise global models of the effects of environmental variables on ecosystem functioning (e.g., Cramer et al., 2001; Diaz et al., 2004) and to improve such models' predictive power.

3. Plant Si as an adaptation to stress

Silicon provides plants with protection from many stresses that are inflicted by the abiotic environment (Cooke and Leishman, 2016) and by pathogens (Fauteaux et al., 2005; Van Bockhaven et al., 2013). Although the mechanisms underlying such protective roles are not always understood, it is now known that these mechanisms vary in their mode of operation. Si can inhibit toxic metal uptake by the root (Ma et al., 2015) and improve the acquisition of beneficial and essential minerals such as phosphorus (Ma and Takahashi, 1990; Gao et al., 2011; Neu et al., 2017). Likewise, phytoliths act as physical barriers against pathogen intrusion (Cai et al., 2008). Within the shoot, Si can be bound with toxic metals and thus neutralise them and transport them to specialised compartments (Cocker et al., 1998; Wang et al., 2004), maintain membrane and cell wall stability under stress (He et al., 2010, 2015), and mediate apoplastic and symplastic osmotic gradients (Coskun et al., 2016). In the leaf, Si deposition has been shown to reduce ultra-violet absorbance (Goto et al., 2003; Schaller et al., 2013), to reduce leaf temperature (Wang et al., 2005) and to participate in regulating stomatal conductance (Hattori et al., 2005). More systemically, Si has been shown to promote anti-pathogenic (Cai et al., 2008; Van Bockhaven et al., 2013) and anti-oxidative activity (Fialova et al., in press; Gong et al., 2005; He et al., 2010), root growth under drought stress (Hattori et al., 2005), stress signalling (Van Bockhaven et al., 2013) and to regulate the expression of some genes that are associated with stress tolerance (Fauteaux et al., 2006; Rios et al., 2017).

Phytoliths and other Si deposits within plant tissues are known to have antiherbivory roles in plants. These structures' rigidity increases plant tissue abrasiveness (Massey and Hartley, 2006; Massey et al., 2006, 2007a; Wiczorek et al., 2015a). Thus, phytoliths and Si deposits can damage herbivore mouth parts, mostly by eroding or wearing them. This has been demonstrated both on invertebrate (Massey and Hartley, 2009; Massey et al., 2006) and vertebrate (Rivals et al., 2014; Wiczorek et al., 2015a) herbivores, although damage degree may vary among herbivore species (Sanson et al., 2007). Plant Si structures also physically protect cell contents, hence reducing herbivores' ability to fully extract and digest cells' organic content (Hunt et al., 2008; Massey and Hartley, 2006, 2009; Wiczorek et al., 2015a). Moreover, it is also feasible that Si that is ingested by herbivores occupies stomach volume that could have been occupied by nutritional organic compounds, hence increasing satiety sensation relative to actual nutritional value. Consequently, some herbivores show low preference for Si-rich plant

foods (Massey and Hartley, 2009; Massey et al., 2006) and to have slower growth rates when feeding on Si-rich diets (Frew et al., 2017a, 2017b; Massey and Hartley, 2006, 2009; Kvedaras et al., 2007; Wiczorek et al., 2015a).

The other way around, herbivory by invertebrates and vertebrates (Hartley and DeGabriel, 2016; Massey et al., 2007b) has been shown to induce Si uptake and accumulation by grasses. Although the degree of induction varies among herbivore types and may be masked by the involvement of other environmental conditions or by grazing history (Katz et al., 2014; Quigley and Anderson, 2014; Soininen et al., 2013), it appears to have a cumulative effect and be stronger with increasing herbivory duration or frequency. *Festuca ovina* and *Lolium perenne* plants that were subjected to repeated damage by locust and voles contained 2–4 times more Si than plants that were subjected to a single damage event (Massey et al., 2007b). This interaction has some intriguing outcomes. First, some grass species have been shown to have as much as twice the Si contents in more heavily grazed localities (Brizuela et al., 1986), while similar patterns are not found in plant species with lower Si contents (Katz et al., 2014). Second, if plant species differ in their ability to take up and accumulate Si as a defence, their competitive ability may depend on Si supply (Garbuzov et al., 2011). Third, herbivore population cycles have been found to be driven by grass Si contents and to be synchronised with plant Si content cycles (Hartley, 2015; Massey et al., 2008; Wiczorek et al., 2015b). Thus, plant Si content does not only affect the plant, but also its neighbours and herbivores, and thus ecosystem-level components and processes.

4. Plant Si in ecosystems and the ecosphere

Silicon's many roles in plant physiology suggest that inter- and intra-specific variability in plant Si contents, uptake and accumulation capabilities – as well as Si roles and functions in plant–environment interactions – may affect how plant communities are assembled and partly determine their properties (e.g., structure, species composition and interaction networks). Nevertheless, evidence for this is still scanty. Brizuela et al. (1986) demonstrated how higher grazing intensity increases Si contents in grass species. Garbuzov et al. (2011) demonstrated how locust prefers grass species with lower Si contents, which are more palatable, resulting in them having smaller biomass and becoming less competitive compared with grass species that accumulate more Si under similar conditions. Jacobs et al. (2013) demonstrated how Si availability facilitates the formation and maintenance of grass-dominated vegetation in tidal marshes and estuaries. Finally, observations that Si-rich habitats are more frequently dominated by grasses while calcium-rich habitats are more frequently dominated by legumes (Schaller et al., 2016b) enabled developing a theoretical model that explains the succession from legume-dominated to grass-dominated pasture lands. Calcic minerals are more easily erodible and thus calcium is more available in early successional stages providing an advantage for legumes, but over time calcium leaches out of the ecosystem while Si accumulates, shifting the advantage towards grasses (Schaller et al., 2017).

By extension, the fact that Si uptake, accumulation and functions vary among taxa (Katz, 2014) suggests that Si availability can partially determine the relative abundance and ecological advantage of grasses over species that take up and accumulate less Si and utilise it less. Therefore, it can modulate plant community structure and composition (e.g., as proposed by Schaller et al., 2017), and eventually community-level adaptation to abiotic environmental conditions (e.g., Cooke and Leishman, 2016) and herbivory (e.g., Massey et al., 2007a). Furthermore, herbivores may prefer to graze in plant communities with lower Si contents (Frew et al., 2016, 2017a; Hunt et al., 2008; Massey and Hartley, 2006, 2009), or themselves suffer from lower growth rates and population growth when grazing in plant communities with high Si contents (Hartley, 2015; Massey et al., 2008). Hence, Si availability and its uptake and accumulation in plants can favour herbivore and animal

communities with species that are more adapted and less affected by Si-rich diets.

However, the effects of plant Si uptake and accumulation clearly exceed the community level and affect ecosystems. Like other elements and nutrients that comprise parts of organismal tissues, Si is also recycled in ecosystems, with plants playing a key role in the process (Carey and Fulweiler, 2012; Struyf et al., 2009). Plants take up Si from the soil as monosilicic acid (H_4SiO_4) and eventually release it back to the soil in detritus as monosilicic acid or as amorphous silica (Alexandre et al., 2011; Cornelis et al., 2010; Farmer et al., 2005). Through their ability to take up and release Si, plants mobilise Si and take part in its export from terrestrial ecosystems to rivers, lakes and oceans (Carey and Fulweiler, 2012; Conley and Carey, 2015; Cornelis et al., 2010; Derry et al., 2005; Struyf et al., 2009). The amount of dissolved Si released from plant litter ranges from 3 to 8 t $\text{km}^{-2} \text{yr}^{-1}$ in forests and saltmarshes (Jacobs et al., 2013). In Hawaiian forest, for example, it is estimated that 68–90% of Si carried by stream water has passed through phytoliths (Derry et al., 2005). Plants can therefore increase Si availability downstream, facilitating conditions for aquatic Si accumulating plants and diatoms (Derry et al., 2005; Farmer et al., 2005; Jacobs et al., 2013; Ronchi et al., 2013; Schoelynck et al., 2014; Vandevenne et al., 2013). Pastures and grasslands, for example, can export as much as 2 t dissolved Si $\text{km}^{-2} \text{yr}^{-1}$ to adjacent rivers (Vandevenne et al., 2013). Such processes of increasing Si availability may have played a role in promoting the evolution of Si-accumulating plants and algae (Falkowski et al., 2004; Katz, 2015).

The global Si and C cycles are sometimes thought to be coupled, since plants' role in Si cycling forms three C sinks. First, Si accumulation improves plant performance (see review in previous section). Carey and Fulweiler (2012) have shown that Si-rich biomes tend to have higher NPP than Si-poor biomes, and calculated that they account for 55% of global terrestrial NPP and CO_2 regulation. Second, by taking up large amounts of labile (dissolved) Si from the soils and accumulating it as amorphous silica, plants may considerably change the stoichiometric balance between dissolved and mineral Si phases and accelerate silicate dissolution (Alexandre et al., 1997; Borrelli et al., 2010; Carey and Fulweiler, 2016; Cornelis and Delvaux, 2016; Farmer et al., 2005; Hinsinger et al., 2001), a process that consumes atmospheric CO_2 (Exley, 1998; Schuiling and Krijgsman, 2006; Song et al., 2012; Street-Perrott and Barker, 2008). Third, some of the organic C produced by plants can be occluded within phytoliths, thus potentially becoming sequestered within soils and sediments for as much as millennia (Alexandre et al., 2015, 2016; Li et al., 2013; Song et al., 2012, 2017). However, the contribution of this latter sink to the global C cycle is disputed. Santos and Alexandre (2017) suggest that post-depositional processes such as oxidation and mineralisation considerably reduce the amount of phytolith-occluded C that is actually stored for such long time periods. Reyerson et al. (2016) suggest that the source of some phytolith-occluded C is from the soil itself, i.e., that it is transferred between pools rather than reflecting net sequestration. Furthermore, Song et al. (2017) estimated phytolith-related C sequestration in global terrestrial biomes at 0.0428 Gt C yr^{-1} , suggesting it contributes little to the global terrestrial sink of 1.9 Gt C yr^{-1} (Quere et al., 2016).

Global models of plant Si effects on the C cycle are still at their infancy, and some major temporal and spatial variations need to be resolved. In the short run plant Si uptake and accumulation removes and sequesters atmospheric CO_2 , whereas in the long run it is possible that Si's roles in improving plant performance and Si:C trade-offs may result in plants improving their C use efficiency and reducing their CO_2 consumption. Furthermore, silicon uptake affects litter chemical properties and thus accelerates decomposition rates (Marxen et al., 2015; Schaller and Struyf, 2013; Schaller et al., 2014). Schaller and Struyf (2013) found that *Phragmites australis* litter mass loss after 6 weeks was 2% and 18% for plants grown without and with Si, respectively. Marxen et al. (2015) found that rice straw lost 60% and 68% of its carbon after 33 days in a litterbag. These suggest that plant Si uptake is not only a C

sink but also a source. Likewise, the relative contributions of various biomes to the C cycle through the three abovementioned sinks vary greatly, as some recent studies have shown (Carey and Fulweiler, 2012; Song et al., 2017). Phytolith carbon sequestration fluxes are approximately 1–1.5 t $\text{CO}_2 \text{km}^{-2} \text{yr}^{-1}$ in forests and 3–4 t $\text{CO}_2 \text{km}^{-2} \text{yr}^{-1}$ in croplands, with little variation among continents, while grassland fluxes range from approximately 1 t $\text{CO}_2 \text{km}^{-2} \text{yr}^{-1}$ in Europe and North America to 2.5–3 t $\text{CO}_2 \text{km}^{-2} \text{yr}^{-1}$ in South America and Australia (Song et al., 2017). Therefore, the causal networks underlying biome- and global-scale processes and variations in Si–C interactions are still ambiguous. Moreover, the effects of plant Si uptake and accumulation on the C cycle are the results of multiple mechanisms acting at multiple scales (from individual plants to ecosystems), responding to multiple abiotic and biotic variables, and playing various roles in plant biology and ecology (e.g., climate, soil, herbivory and pathogeny). Therefore, understanding and predicting how environmental changes may affect plant Si uptake and accumulation at the regional to global scales and what are the consequences for the C cycle remains a formidable challenge.

5. An evolutionary perspective

Extant species and ecosystems are the result of long-term deep-time evolutionary processes. These processes can therefore explain whether or how extant species and ecosystems are adapted and may respond to environmental change (Benton and Emerson, 2007; Crisp et al., 2009; Lamsdell et al., 2017; Wiens and Donoghue, 2004). Phytoliths' preservation in soils and sediments makes them a powerful tool for reconstructing past vegetation formations, mostly during the Cainozoic (e.g., Bremond et al., 2004; Coe et al., 2017; Feng et al., 2017; Li et al., 2018; Strömberg, 2004, 2005; Strömberg et al., 2013) and in archaeological studies (e.g., Katz et al., 2007; Tsartsidou et al., 2008), and potentially also in deeper time.

Nevertheless, the roles plant Si itself played in the evolutionary history of plants, their adaptation to abiotic and biotic environmental conditions, and plant–herbivore interactions remain obscure and disputed. A vibrant discussion in recent years revolves around the possible role of plant Si in the global expansion of the grassland biome on several continents during the mid-late Cainozoic (Edwards et al., 2010; Strömberg, 2011). Although atmospheric changes (CO_2 concentration decrease, cooling and drying) are usually taken as the key initiators of this expansion, reinforcement by ecological processes is also proposed (Beerling and Osborne, 2006; Edwards et al., 2010; Kürschner et al., 2008). Plant Si is sometimes thought to have played an appreciable part in grassland evolution and expansion, due to its roles in protecting plants from drought (Coskun et al., 2016; Gong et al., 2005; Zhu and Gong, 2014) and herbivory (Frew et al., 2017a; Hartley and DeGabriel, 2016; Massey and Hartley, 2006, 2009; Massey et al., 2007a). One of the driving and reinforcing ecological processes is a putative co-evolutionary escalation between Si-rich grasses and large mammalian herbivores possessing abrasion-adapted dentition (MacFadden, 1997; Stebbins, 1981). Recent evidence challenge the significance of this putative co-evolution. Northern hemisphere grasslands predate mammalian abrasion-adapted dentition by several million years (Mühlbachler et al., 2011; Solounias and Semperebon, 2002; Strömberg, 2005, 2006, 2011), whereas in South America mammalian abrasion-adapted dentition predates grasslands by several million years (Dunn et al., 2015). Hence, there appears to be no clear coalescence in the evolution of grasslands and mammalian abrasion-adapted dentition, nor a consistent order of events, as would be expected if the two traits co-evolved or if one evolved as result of the other.

More recently, attempts have been made to trace the early origins and evolution of Si accumulation among angiosperms, using molecular phylogenies. Strömberg et al. (2016) found that emergence dates of Si-rich clades do not coalesce with any likely selective force, including herbivory, habitat openness, aridity and atmospheric CO_2 decline.

Nevertheless, gene divergence times often overestimate clade divergence times and do not reflect trait emergence or ecological success (Katz, 2015, 2018). Taking this into account, Katz (2015) suggested that the independent early diversification of Si-rich angiosperm clades may be dated to the Late Cretaceous and be linked in part to the simultaneous evolution of abrasion-adapted dentition in some dinosaur and early mammalian groups. Ancestral grass phytoliths in a coprolite produced by an herbivorous dinosaur from the Late Cretaceous (Prasad et al., 2005), and more recently and more interestingly the abrasion-adapted dentition of an Early Cretaceous dinosaur (Wu et al., in press) fit this hypothesis. Improving our understanding on how plant Si uptake and accumulation corresponds to environmental variations and affect other ecosystem components will allow us to more critically test such hypotheses using quantitative data and models.

The evidence for Si:C trade-offs (Cooke and Leishman, 2012; Schaller et al., 2012a, b; Schoelynck et al., 2010), the observed effects of atmospheric CO₂ concentrations on plant Si contents (Johnson and Hartley, in press) and that low atmospheric CO₂ concentration remains a possible prerequisite for grassland expansion (Strömberg, 2011) imply that Si accumulation can confer an advantage to Si-rich clades like the grasses in a low CO₂ environment. This unexplored possibility suggests that the current increase in atmospheric CO₂ concentrations may impair the competitive ability of grasses and other Si-rich plants worldwide.

6. Implications and future directions

The surge of studies of plant Si accumulation has clearly demonstrated Si's many roles in plant life – providing them with mechanical support and protection from a multitude of abiotic and biotic stresses – and its effects on plant performance, plant community structure and ecosystem- and global-scale processes. Hidden in plain sight, plant Si content is a plant functional trait linking environmental conditions with ecological functioning. Achieving a better understanding of the mechanisms by which plant Si content responds to environmental change and affects ecological functioning at various spatial and temporal scales, will surely improve the predictive power of models of climate change effects on ecosystem structure and functioning (e.g., Cramer et al., 2001).

However, since research of plant Si is not yet as developed as research of other plant functional traits, some theoretical gaps still hinder us from achieving this goal. The roles of plant Si in plant biology are not fully explored (Cooke and Leishman, 2011a; Katz, 2014, 2015), and may vary among taxa (Katz, 2014). Although understanding the evolutionary history of this trait may signify a leap forward in the latter matter, it remains largely elusive (Katz, 2015; Strömberg et al., 2016). Possible interactions of plant Si content with other plant functional traits have been explored only recently, and their sources and consequences are little understood (Cooke and Leishman, 2011a, 2011b, 2012; Schaller et al., 2012a, 2012b, 2016a; Schoelynck et al., 2010; Song et al., 2014). The biological mechanisms that underlie intra-specific variations in plant Si content along environmental gradients are unclear (Katz et al., 2013, 2014, in press; Quigley and Anderson, 2014; Soininen et al., 2013), in part due to discrepancies between controlled experiments and field studies (Katz et al., in press). Consequently, we still have relatively little understanding of how plant Si contents vary among ecosystem types and biomes in response to environmental conditions and how these variations affect variations in ecosystem functioning (Carey and Fulweiler, 2012; Jacobs et al., 2013; Schaller et al., 2017). Acquiring sufficient data and knowledge to fill these gaps will contribute to our understanding of plant community assembly and structure and of ecosystem functioning. Incorporating plant Si into models of ecosystems' and global biogeochemical cycles' responses to climate change, once appropriate data exists, is very likely to improve such models' predictive power and hence our ability to predict and mitigate climate change effects on ecosystems and global biogeochemical cycles.

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